Dietary restriction would probably not increase longevity in human beings and other species able to leave unsuitable environments

Éric Le Bourg

Abstract This article argues that dietary restriction would not increase longevity in species able to leave a place where they are subjected to starvation. Human beings can emigrate when feeding conditions are a threat to survival and thus they would not live longer if subjected to dietary restriction.

Key-words Dietary restriction · Longevity · Human beings · Evolution · Life history

Dietary restriction does not increase longevity in all species

Dietary restriction (DR) increases longevity of rodents (Bertrand et al. 1999), in fishes (e.g. Woodhead 1985) and various invertebrate species (e.g. Fanestil and Barrows 1965; Klass 1977; Verdone-Smith and Enesco 1982; Austad 1989), but not in the flies Musca domestica (Cooper et al. 2004) and Ceratitis capitata (Carey et al. 2002, but see Carey et al. 2005), in some rotifer species (Kirk 2001) and in the butterfly Speyeria mormonia (Boggs and Ross 1993).

Concerning the fruitfly Drosophila melanogaster, negative and positive results have been reported (review in Le Bourg and Minois 2005). Le Bourg and Minois (2005) have criticized the DR procedures used by Linda Partridge and her collaborators and concluded that the claim for a longevity increase was probably not justified.

Bodkin et al. (2003) reported that DR increases longevity in Rhesus monkeys, but this article has been criticized (Lane et al. 2004; but see Bodkin et al. 2005), particularly because only 8 animals were subjected to DR (vs. 109 animals in three control groups). By contrast, no positive effect of DR on longevity in Rhesus monkeys has been observed by Ingram et al. (2005): at least 12 years after the onset of DR experiments (17 years for some animals, n > 80), 50% of the control monkeys had died, the very same percentage being observed in monkeys subjected to DR. Such a result is clearly not in favor of a positive effect of DR on human longevity, provided that monkeys and humans would respond similarly to DR. As new results on primates under DR will be probably published, the time is ripe to wonder whether DR could increase longevity in human beings, particularly because some volunteers are already practicing DR (http://www.calorie-restriction.org/).

This article describes a hypothesis based on evolutionary constraints to predict that DR would not increase longevity in human beings and explains why DR does not increase lifespan in some species. This
hypothesis complements other hypotheses reaching the same conclusion about human longevity (e.g. de Grey 2005; Demetrius 2004; Phelan and Rose 2005) and does not contradict the hypothesis that responses to DR are an evolutionary adaptation to starvation (e.g. Holliday 1989; Masoro and Austad 1996; Shanley and Kirkwood 2000) but, rather, reinforces this conclusion.

The hypothesis

After birth, *ad libitum*-fed mammals grow up to adulthood when they begin to reproduce. Reproduction can last for a short or long time, depending on the occurrence of death due to predators, diseases, or other life-threatening events. However, it may also happen that this Normal Program (Le Bourg 2003) is disturbed by starvation. If subjected to starvation, mammals may stop or lower growth if they are young, or delay and decrease reproduction if they have reached adulthood. This Rescue Program allows mammals to survive until adverse conditions are over. In other words, growth and reproduction are temporarily sacrificed to allow survival, because this life-history strategy is preferable to one allowing reproduction with a too weak metabolic supply (Stearns 1992). This Rescue Program is not limited to mammals and is tuned to the characteristics of each species. Hence, food restriction also decreases fecundity in *D. melanogaster* (e.g. David et al. 1971), in the butterfly *Speyeria mormonia* (Boggs and Ross 1993), and in the spider *Frontinella pyramitela* (Austad 1989). Another way to cope with starvation is shown by the nematode *C. elegans* entering the dauer non-feeding larval stage during which reproduction is impossible (Klass and Hirsh 1976).

Animals subjected to food restriction, if its level is not too high, often live longer than *ad libitum*-fed ones but this pattern is not always observed: why?

Masoro and Austad (1996) made the hypothesis that species not facing short-term unpredictable food shortages could have lost their ability to respond to DR. For instance, vegetation-consuming monkeys living in tropical forests could not show a longevity increase when subjected to DR. Going a step farther, it could be that species able to avoid the negative consequences of such a food shortage by implementing a behavioral strategy could not live longer if subjected to DR. The best mean not to suffer from a food shortage in a given biotope is simply to leave it... if it is possible. Species able to flee could thus not live longer when subjected to DR because fleeing would be less costly than decreasing fecundity, increasing stress resistance and increasing longevity in presence of starvation. With such a hypothesis, it is possible to predict which species would live longer when subjected to DR and those which would not.

The first category comprises species able to flee. Flies subjected to starvation in a given place can move to another one offering better living conditions and, in accordance with the hypothesis, DR does not seem to increase longevity in *M. domestica* (Cooper et al. 2004) and *C. capitata* (e.g. Carey et al. 2002). Using DR procedures combining stochastic food availability and its persistence, Carey et al. (2005) reported longevity increases in some cases and concluded that a longevity increase was not a universal response to DR because “the longevity response is highly sensitive to the particular method of restriction”. Concerning *D. melanogaster*, most of claims for longevity increases under DR cannot be considered as justified (review in Le Bourg and Minois 2005). Therefore, it seems that flies do not live longer under DR.

As far as I know, no DR experiment has been performed in flying birds. These species can easily escape from places where food is unsufficient to sustain life and this is exactly what migratory birds do before winter. During the hot season, flying birds can avoid unsuitable environments, simply by moving. The same considerations could be applied to other species able to leave inappropriate environments and human beings seem to belong to this category. During the past centuries, human populations facing famine usually emigrated, as it was the case for eastern or northern European populations invading the Roman empire or for Irish people emigrating to the USA during the XIXth century. Emigrants had probably a higher chance to survive and reproduce than people staying at home, waiting for an incapable fate: these last people certainly did not break the longevity record of their time. Obviously, the highly predictable winter food shortage does not provoke emigration simply because humans are used to cope with such an event by accumulating food reserves during the hot season. Therefore, since, from their very origin, human beings are used to move